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REVIEW
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Identifying Resistance to the Colorado Potato Beetle (*Leptinotarsa decemlineata* Say) in Potato Germplasm: Review Update

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Developing plant germplasm that contains genetic resistance to insect pests is a valuable component of integrated pest management programs. In the last several decades, numerous attempts have been made to identify genetic sources of resistance to Colorado potato beetle *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae). This review focuses on compiling information regarding general *L. decemlineata* biology, ecology, and management focusing on discussing biochemical and morphological potato (*Solanum tuberosum* L.) plant traits that might be responsible for providing resistance; the review ends discussing past efforts to identify genetic material and highlights promising new strategies that may improve the efficiency of evaluation and selection of resistant material. Measurement strategies, that begin with field screening of segregating populations or wild germplasm to narrow research focus can be useful. Identifying particularly resistant or susceptible germplasm, will help researchers focus on studying the mechanisms of resistance in much greater detail which will help the development of long-term sustainable management program.

Keywords: Chrysomelidae, drones, insects, resistance, sampling, *Solanum*, UAV

INTRODUCTION

Hundreds of crop varieties are released every year to improve crop productivity, enhance nutritional value, and expand consumer choice (Everson and Gollin, 2002); crops are also improved to repel, prevent, block, or eliminate pests (Mohammed et al., 2000; Rondon et al., 2009). Clearly, crop improvement is one of the drivers of crop production and extensive studies have evaluated the contributions of plant breeding to production enhancement in association with marketing and utilization (Douches et al., 1996). However, when we manage pests including insects, diseases, or nematodes, the limitations of biological and other control tactics have pushed producers to rely on the use of pesticides as we will discuss below (Mitkowski and Abawi, 2003; Ramirez et al., 2009; Maharijaya and Vosman, 2015).

In commercial potato, *Solanum tuberosum* L., the Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae), is well-known for rapidly evolving resistance to insecticides (Alyokhin et al., 2008; Schoville et al., 2018), which reinforces its status as one of the most important potato pests (Weber, 2003). Over 300 documented cases of insecticide resistance are listed in the literature coming from Asia, Europe, and North America (Whalon and Mota-Sanchez, 2017; Brevik et al., 2018a,b). Interestingly enough, populations of *L. decemlineata* do not respond equivalently to pesticides; some researchers argue that it may be due to evolutionary differences in how *L. decemlineata* interacts with potatoes within the landscape (Whitaker, 1994; Wierenga and Hollingworth, 1994; Crossley et al., 2019a,b). Others suggest a moderate variation at the nuclear loci level (Hawthorne, 2001; Izzo et al., 2018). Remarkably, in Idaho, Oregon, and Washington which together produce close to 56% of United States fresh and frozen potatoes in the market, *L. decemlineata* populations have largely remained susceptible to insecticides (Haegele and Wakeland, 1932; Johnston and Sandvol, 1986; Olson et al., 2000; Alyokhin et al., 2015; Crossley et al., 2018; Dively et al., 2020). According to Lynch and Walsh (1998), populations with lower genetic variance are expected to adapt more slowly, and *L. decemlineata* in the Northwestern United States exhibits lower genetic diversity than elsewhere which may explain its susceptibility to pesticides. In comparison, populations in other areas like east of the Rocky Mountains, *L. decemlineata* has historically developed pesticide resistance (Grafius, 1995; Grafius and Douches, 2008). Hence, the need to add novel tools in the pest management toolbox to help potato producers manage this pest problem remains and the availability of *L. decemlineata* potato resistant varieties could complement existing management practices.

HOST RANGE AND DISTRIBUTION OF *LEPTINOTARSA DECEMLINEATA*

Leptinotarsa decemlineata is largely considered a pest of Solanaceous crops (Foster, 1876). *Solanum* is a large and diverse genus, including important economic crops with a wide geographical range such as potato, tomato (*S. lycopersicum* L.), and eggplant (*S. melongena* L.) (Whalen, 1979). Hitchner et al. (2008) and Li et al. (2013) studied the host preference of *L. decemlineata* comparing potato to crops such as tomato or eggplant, observing a clear affinity for potatoes. *Leptinotarsa decemlineata* is widespread in North America feeding on several plant species already described above in addition to Solanaceous weeds such as *S. angustifolium* Miller, *S. rostratum* L., and *S. eleagnifolium* Cav., several species of nightshades (*S. dulcamara* L., *S. sarrachoides* L., including hairy nightshade (*S. nitidibaccatum* Bitter; a.k.a. *S. sarrachoides* Sendt or *S. physalifolium* Rusby), and horse nettle (*S. carolinense* L.) (Tower, 1906; Latheef and Harcourt, 1974; Hsiao, 1978, 1981; Hare, 1983, 1990; Hare and Kennedy, 1986; Horton et al., 1988; Jacques, 1988; Weber et al., 1995; Xu and Long, 1995; Mena-Covarrubias et al., 1996). Anecdotical observations that need further investigation suggest that Solanaceous weeds co-exist or overlap with cultivated potatoes in the Northwestern US; however, *L. decemlineata* has a strong preference for cultivated potatoes.

In the US, *L. decemlineata* was *first* associated with Solanaceous plants around 1859, when it was reported on *S. rostratum* in Omaha, Nebraska, near the Iowa border (Casagrande, 1985). By 1859, *L. decemlineata* was found on *S. tuberosum* (Walsh, 1866), and by 1874, *L. decemlineata* spread rapidly eastward reaching the Atlantic coast (Tower, 1906; Hsiao, 1978; Logan et al., 1987; Jacques, 1988; Alyokhin, 2009; Zhao et al., 2013; and Izzo et al., 2018). Member of the genus *Leptinotarsa* have been long known to feed on *S. rostratum* in central Mexico, suggesting Mexico as the center of distribution of *L. decemlineata*. Historically, as the Solanaceous weed geographical range expanded northward, so did *L. decemlineata* distribution (**Table 1**). Worldwide, by the end of the 20th century, *L. decemlineata* was well-established in Europe, Asia Minor, Iran, Central Asia including China (Jolivet, 1991; Weber, 2003; Alyokhin, 2009). In Europe, *L. decemlineata* became established near Bordeaux, France in 1922, and spread throughout the French potato production regions, although it went undetected until 1935 (Hurst, 1975). Hurst (1975) reported three invasions (1876, 1901, 1914) in Great Britain that were "aggressively" (chemically) controlled. Crossley et al. (2017) reported that currently in Europe there are two clades: a western clade (French, Spanish, and Italian) and an eastern one (Poland, Estonia, Finland, and Russia). This information suggests multiple arrivals of *L. decemlineata* in Europe but could also be explained by adaptation to regional environment/hosts or genetic drift within isolated populations. Moving to Asia, *L. decemlineata* populations reached western China by 1993 and now it can be found in several Chinese potato regions (Zhang et al., 2013).

Recently, Izzo et al. (2018) used mitochondrial DNA and nuclear loci to examine the origin of *L. decemlineata* lineages. Authors suggested a genetically heterogenous *L. decemlineata* population which may contribute with contemporary populations. Schoville et al. (2018) used *L. decemlineata* as a model species for agricultural pest genomics that provides a better understanding of the insect and its host information that can be used for future genetic and evolutionary studies.

LIFE HISTORY OF *LEPTINOTARSA DECEMLINEATA*

Adults and larvae of *L. decemlineata* are voracious defoliators of *S. tuberosum*. Ferro et al. (1985) report that approximately 40 and 10 cm^2 of potato leaves are consumed by larvae and adults during their lifetime, respectively. Once leaf tissue is gone, *L. decemlineata* begins feeding on stems and tubers (Weber and Ferro, 1993), before moving into the soil to overwinter.

Coupling insect-host relationships and abiotic factors, *L. decemlineata* can be found in a diverse range of climates (Grapputo et al., 2005; Li et al., 2014). Temperature and humidity during the spring are important for the survival of overwintering populations (Izzo et al., 2014; Li et al., 2014). Pelletier (1995) and Pelletier (1998) indicated that high temperatures thresholds for larvae, pupae, and adults are 49, 61, and 57°C, respectively. Mail and Salt (1933), Hurst (1975), Hiiesaar et al. (2006), Izzo et al. (2014), Li et al. (2014) reported lethal tempertures of -10 to -4°C. Moreover, overwintering survival can be as high as 90% in absence of snow cover (Gibson et al., 1925; Ushatinskaya, 1978; Hiiesaar et al., 2006; Huseth and Groves, 2013). Overwintering

TABLE 1 | Initial historical expansion of *Leptinotarsa decemlineata* Say.

Location	Year*	Host**		References
		Scientific name	**Common name**	
Mexico	?	*Solanum rostratum*	Buffalobur	Casagrande, 1987
		Solanum angustifolium	Nightshade	
USA	1811	?		
	1819–1820	*Solanum tuberosum*	Potato	Casagrande, 1985 Jacques, 1988
Nebraska-Iowa	1859	*Solanum tuberosum*	Potato	Jacques, 1988
Atlantic coast	1874	*Solanum tuberosum*	Potato	Casagrande, 1987
Canada	1874	*Solanum tuberosum*	Potato	Casagrande, 1987
Colorado	1864	*Solanum rostratum*	Buffalobur	Walsh, 1865
Colorado	1874	*Solanum tuberosum*	Potato	Riley, 1869a,b
Germany	1877	*Solanum tuberosum*	Potato	Feytaud, 1938
France	1922	*Solanum tuberosum*	Potato	Feytaud, 1938

may be as short as 30 days (Capinera, 2001), although Biever and Chauvin (1990) observed that 16% of *L. decemlineata* populations could remain in diapause for 2–3 winters in Washington State, while Tauber and Tauber (2002) reported 2.3% of *L. decemlineata* populations overwintering in New York after a 10-year study. After emerging in the spring, *L. decemlineata* disperse by walking or flying (Voss and Ferro, 1990; Follett et al., 1996; Noronha and Cloutier, 1999; Boiteau et al., 2003). Surviving overwintering adults feed, reproduce, lay eggs, and die.

The life cycle consists of an egg stage, four larval stages, pupal, and adult stages. Adults are polygamous, performing multiple copulations (Alyokhin et al., 2015). Depending on temperature, females deposit masses of 20–60 yellowish-orange eggs (Isely, 1935; Hare, 1983, 1990). Each female may lay up to 800 eggs during her lifetime (Brown et al., 1980; Ferro et al., 1985). Eggs are attached to plant tissue, although recently we have observed that certain potato varieties inhibit this process. All eggs hatch simultaneously, and larvae immediately feed until reaching the pupal stage (Hazzard et al., 1991) (**Figure 1**). Pupation occurs in the soil (Hare, 1983), and adults emerge 5–7 days later, depending on temperature. They then start a new cycle of dispersing, feeding, mating, and egg laying. Life cycle last 30 days depending on temperatures. Depending on geographical location and climatic conditions, 2–3 generations per year are completed (Walgenbach and Wyman, 1984; Ferro et al., 1985; Xu and Long, 1997).

CURRENT MANAGEMENT PRACTICES

Core management of *L. decemlineata* focuses on chemical, cultural, and biological control.

Chemical control has been largely studied (Grafius, 1995, 1997; Wustman and Carnegie, 2000; Zabel et al., 2002; Stankovik et al., 2004; Alyokhin et al., 2008; Grafius and Douches, 2008; Alyokhin, 2009; Sladam et al., 2012; Szendrei et al., 2012; Piiroinen et al., 2014; Clements et al., 2016). Although insecticides are effective, resistance has been an issue in many populations (Casagrande, 1987; Kennedy and Farrar, 1987; Helm et al., 1990; Grapputo et al., 2005; Alyokhin et al., 2006, 2008; Szendrei et al., 2012; Kaplanoglu et al., 2017; Clements et al., 2018; Crossley et al., 2018), while other populations have largely remained susceptible to insecticides (Haegele and Wakeland, 1932; Johnston and Sandvol, 1986; Olson et al., 2000; Alyokhin et al., 2015; Crossley et al., 2018; Dively et al., 2020).

Crop rotation (Lashomb and Ng, 1984; Weisz et al., 1994; Speese Iii and Sterrett, 1998; Sexson and Wyman, 2005; Sexson et al., 2005; Huseth et al., 2012), the use of plastic-lined trenches (Boiteau and Vernon, 2001), straw mulch (Stoner et al., 1996; Stoner, 1997), trap cropping (Hunt and Whitfield, 1996; Hoy et al., 2000), thermal control (Rifai et al., 2004), and electromagnetic control (Colpitts et al., 1992) are a few examples of cultural, mechanical and physical control options. Interestingly, combining the dispersal behavior of *L. decemlineata*, which despite their ability to fly mainly disperse by walking, and the rotation of potato fields with non-host crops can reduce adult abundance (Follett et al., 1996; Hough-Goldstein and Whalen, 1996; Sexson and Wyman, 2005). More recently, Crossley et al. (2017, 2019a,b) discussed the effect of land cover composition influencing the efficacy of crop rotation such as higher wheat land in the Northwest and forest field edges in the Central Sands of the US. These studies suggest the importance of land coverage in *L. decemlineata* movement and distribution and further studies are currently underway in the Northwest.

Some field studies suggest that natural enemies have minimal effect (Chang and Snyder, 2004; Koss et al., 2004, 2005). However, predators such as the Carabidae *Pterostichus melanarius* Illiger (Alvarez et al., 2013, Rondon et al., 2013) and the Chrysopidae *Chrysoperla carnea* Stephens (Sablon et al., 2013) were found feeding on *L. decemlineata*. Two Tachinidae parasitic flies, *Myiopharus aberrans* L. and *M. doryphorae* Riley (**Figure 2**) were found to parasitize *L. decemlineata* with relative success (Kelleher, 1966; Tamaki et al., 1982, 1983; Gollands et al., 1991; Lopez et al., 1993, 1997). Several species of *Bacillus*

FIGURE 1 | *Leptinotarsa decemlineata* larva.

including *B. pumilus* L., *B. cereus* Frankland and Frankland, *B. megaterium* de Bary (Ertürk et al., 2008), and *B. thuringiensis* Berliner (Walker et al., 2003; Whalon and Wingerd, 2003; Gassmann et al., 2009; Wraight and Ramos, 2015) were found to cause *L. decemlineata* mortality. Although the real impact of natural enemies controlling *L. decemlineata* is unknown, studies by Snyder and Clevenger (2004) and Lynch (2013) exploring the consumption by two generalist predators in potatoes using molecular gut content analysis and behavioral studies could provide new insights into host selection and role of microbiota into *L. decemlineata* fitness and sucess. For additional information about natural enemies see **Table 2**.

HOST SELECTION BY *L. DECEMLINEATA*: THE NEED FOR "WILD RELATIVES"

In herbivores, chemical signals have an important role in host plant selection (Fürstenberg-Hägg et al., 2013; Sablon et al., 2013; Wen et al., 2019). Volatiles like trans-2-hexen-1-ol-hexanol, cis 3-hexen-1-ol, trans-2 hexenal, and linalool, methyl salicylate, and z-3-hexenyl acetate have been reported as key cues for *L. decemlineata* (Visser et al., 1979; Dickens, 2000, 2002; Martel et al., 2005). Moreover, damaged leaves potentially produced and releases additional chemicals that may attract *L. decemlineata* (Boiteau et al., 2003). Stimulants, or essential dietary components produced by potato plants, released by potato plants such as sterols (e.g., cholesterol, b-sitosterol, stigmasterol) and sucrose, melezitose, glucose and fructose, amino acids, phospholipids, and chlorogenic acid (Hsiao, 1969) act as feeding stimulants (Szafranek et al., 2008); conversely, flowers of tansy (*Tanacetum vulgare* L.) which contain high levels of camphor and umbellulone, act as feeding deterrents (Yencho et al., 1994, 1996, 2000; Pelletier and Dutheil, 2006; Maharijaya and Vosman, 2015). Based on this information, manipulation of chemical cues which may affect "normal" behavioral choices of *L. decemlineata* potentially could be deployed via plant breeding to regulate feeding behavior and manipulate their control. A summary of current efforts will be discussed below.

FIGURE 2 | *Myiopharus doryphoae* (Diptera: Tachinidae) parasitoid of *Leptinotarsa decemlineata*.

PLANT BREEDING

Plant breeding is a powerful tool that can contribute to pest management. The notion of utilizing variation in *L. decemlineata* host preference between potato varieties (Torka, 1950; Horton et al., 1997; Metspalu et al., 2000) for breeding has been considered since the late 19th century (Saunders and Reed, 1871; Chavez et al., 1988). However, the potential to improve insect resistance by breeding within domesticated potato alone is limited due to potato narrows genetic base (Hardigan et al., 2017; Jansky and Spooner, 2018). Fortunately, the germplasm pool of approximately 107 *Solanum* spp. related to potato comprises one of the deepest and most accessible sources of pest resistant alleles among all major crops (Spooner and Bamberg, 1994; Jansky et al., 2013; Spooner et al., 2014; Bethke et al., 2017) (**Table 3**). Systematic field screens aimed at identifying crop wild relatives that exhibit *L. decemlineata* resistance have been performed on large scales by several investigators since the early 1930s (Torka, 1950), with the efforts of Carter (1987), Flanders et al. (1992), and Jansky et al. (2009) all making major contributions to our knowledge on this topic at a species and accession level (Pelletier et al., 2011).

Foliar production of phytochemical insect toxins (often glycoalkaloids) is one major mechanism of *L. decemlineata* resistance found in potato wild relatives (Buhr et al., 1958; Andersson, 1999). Total foliar concentration of α-solanine and α-chaconine, the primary glycoalkaloids found in domesticated potato, are poor predictors of plant *L. decemlineata* resistance (Barbour and Kennedy, 1991; Flanders et al., 1992; Metspalu et al., 2000; Dinkins et al., 2008; Navarre et al., 2016) likely because they are not accumulated in high enough concentrations to inhibit insect feeding (Sinden et al., 1980; Friedman et al., 1997). Instead, insect resistance has often been linked with the production by lower abundance glycoalkaloids found in wild potato relatives (Tingey, 1984; Kowalski et al., 1999, 2000) that exhibit structural differences in their nitrogen containing 27-carbon cholestane aglycone backbone and variation of the hydrophilic carbohydrate side chain attached to 3-OH position of the aglycone molecule (Friedman et al., 1997; Milner et al., 2011). In total, more than 90 structurally unique steroidal alkaloids have been identified from roughly 350 wild potato species (Friedman

TABLE 2 | Natural enemies of *Leptinotarsa decemlineata*.

Natural enemies	Order	Family	Genus	Species	Region	References
Predator	Neuroptera	Chrysopidae	*Chrysopa*	*carnea* Stephens	Midwest	Heimpel and Hough-Goldstein, 1992
	Hemiptera	Pentatomidae	*Podisus*	*maculiventris* Say	Midwest	Heimpel and Hough-Goldstein, 1992; Hough-Goldstein et al., 1993; Brust, 1994; Hough-Goldstein and McPherson, 1996
			Perillus	*nioculatus* Fabricius	Midwest	Heimpel and Hough-Goldstein, 1992; Brust, 1994; Hough-Goldstein and McPherson, 1996
		Nabidae	*Nabis*	*alternatus* Parshley	Northwest	Koss et al., 2005; Crowder et al., 2010; Lynch, 2013
		Geocoridae	*Geocoris*	*bullatus* Say	Northwest	Koss et al., 2005; Crowder et al., 2010; Lynch, 2013
	Coleoptera	Coccinellidae	*Coleomegilla*	*maculate* De Geer	Midwest	Groden et al., 1990; Hazzard et al., 1991; Heimpel and Hough-Goldstein, 1992; Brust, 1994
			Hipodamia	*convergens* Guérin-Méneville	Northwest	Koss et al., 2005; Crowder et al., 2010
		Carabidae	*Lebia*	*grandis* Hentz	Midwest	Groden, 1989; Heimpel and Hough-Goldstein, 1992; Brust, 1994
			Pterostichus	*melanarius* Illiger	Northwest	Koss et al., 2005; Crowder et al., 2010; Alvarez et al., 2013; Rondon et al., 2013
Parasitoid	Diptera	Tachinidae	*Myiopharus*	*doryphorae* Riley *aberrans* Townsend	Continental US and Canada	Kelleher, 1966; Tamaki et al., 1982, 1983; Gollands et al., 1991; Hough-Goldstein et al., 1993; Lopez et al., 1993, 1997; Fraval, 2001
Pathogens	Hypocreales	Codycipitaceae	*Beauveria*	*bassiana* (Bals.-Criv) Vuill		Campbell et al., 1985; Anderson et al., 1989; Armer et al., 2004; Ramirez et al., 2009; Crowder et al., 2010
	Rhabditida	Heterorhanditidae	*Heterorhabditis*	*megidis* Poinar, Jackson and Klein		
		Steinernematidae	*Steinernema*	*carpocapsae*		

et al., 1997; Pelletier et al., 2001; Shakya and Navarre, 2008; Milner et al., 2011; Mweetwa et al., 2012; Tai et al., 2014).

The significance of leptine class glycoalkaloids as a feeding deterrent has long been recognized as a potential source of *L. decemlineata* resistance (Sinden et al., 1986a,b). Leptines I and II are triose glycosides derived from a solanidane precursor which are differentially acetylated to contain either an acetoxy or hydroxyl moiety the C23 position of the aglycone backbone (Friedman et al., 1997; Ginzberg et al., 2009; Milner et al., 2011; Pelletier et al., 2011). Leptine molecules are only found in a few accessions of *S. chacoense* and are perceived to deter insect feeding through cholinesterase inhibition and cell membrane disruption within the insect (Sinden et al., 1986a, 1988; Wierenga and Hollingworth, 1994; Sanford et al., 1997; Rangarajan et al., 2000; Yencho et al., 2000; Lorenzen et al., 2001). Introgression of leptine biosynthesis into domesticated potato is an attractive breeding objective as leptines are only produced in foliar tissues and do not accumulate within tubers (Sinden et al., 1986a; Sanford et al., 1996; Mweetwa et al., 2012).

Breeding work on this trait has largely focused on mapping of resistance found in the diploid *S. chacoense* accession USDA8380-1 (Sinden et al., 1986a; Ronning et al., 1998; Hutvágner et al., 2001; Boluarte-Medina et al., 2003; Kaiser et al., 2020) and a few tetraploid *S. tuberosum* introgression lines (Lorenzen et al., 2001). Leptine content segregates as a multi-locus, additive trait in both diploid and tetraploid backgrounds. Contemporary studies that leverage the power of molecular genotyping tools in biparental linkage mapping populations have identified major QTL associated with leptine abundance on chromosomes 1, 2, 6, 7, and 8 (Ronning et al., 1998; Hutvágner et al., 2001; Boluarte-Medina et al., 2003; Manrique-Carpintero et al., 2014; Kaiser et al., 2020). Somewhat surprisingly the proportion of variance attributed to major QTL located on chromosome 1 (Ronning et al., 1999; Hutvágner et al., 2001; Boluarte-Medina et al., 2003; Manrique-Carpintero et al., 2014) and chromosome 2 (Sagredo et al., 2009; Kaiser et al., 2020) have varied by study. This may be attributed to the structure of the linkage mapping population or due to genetic epistasis between genomic backgrounds.

Other glycoalkaloid compounds are also known to play prominent roles in plant defense against *L. decemlineata*, but less is understood regarding inheritance of pathway components at a molecular genetics level. Dehydrocommersonine and solanidenol-chacotriose concentration has been demonstrated to play opposing roles in *L. decemlineata* resistance when inherited from *S. oplocense* (Tai et al., 2015; Paudel et al., 2019). Selective genotyping of a *S. oplocense* × *S. tuberosum* F1 population have mapped a QTL associated with production of these molecules to a location on chromosome 1 (Paudel et al., 2019) also identified in a *S. berthaultii* × *S. tuberosum* F1 population by Yencho et al. (1998). Correlative evidence supporting association between *L. decemlineata* resistance of wild species and other glycoalkaloid molecules found in potato is intriguing but less direct in so far as proven causation.

The structure and abundance of glandular trichomes are another biological characteristic that contributes to insect resistance in *Solanum* spp. (Gibson, 1971; Gibson and Turner, 1977; Tingey and Gibson, 1978; Tingey and Sinden, 1982;

TABLE 3 | Wild *Solanum* species of potato exhibiting resistance to *Leptinotarsa decemlineata*.

Species	Resistance factor	Mechanism of resistance	Ploidy and (EBN)	References
S. pinnatisectum		Antixenosis	2X (1EBN)	Pelletier et al., 1999; Chen et al., 2003; Li et al., 2006
S. polyadenium	Trichomes	Antibiosis	2X	Pelletier et al., 1999, 2001; Fréchette et al., 2010
S. albornozii			2X (2EBN)	Jansky et al., 2009
S. immite			2X (1EBN)	Jansky et al., 2009
S. chacoense	Leptines, leptinine	Antibiosis	2X (2EBN)	Sanford et al., 1996; Yencho et al., 2000; Hutvágner et al., 2001; Sagredo et al., 2009; Mweetwa et al., 2012
S. berthaultii	Trichomes Methyl chloride		2X (2EBN)	Pelletier et al., 1999, 2001 Yencho et al., 1994
S. neorossii			2X	Jansky et al., 2009
S. jameseii		Antixenosis/antibiosis	2X (1EBN)	Pelletier et al., 1999, 2001
S. tarijense	Trichomes, volatile compounds on trichomes	Antibiosis/antixenosis	2X (2EBN)	Pelletier et al., 1999, 2001; Pelletier and Dutheil, 2006; Fréchette et al., 2010
S. chardiophyllum			2X (1EBN)	Jansky et al., 2009
S. commersonii			2X (1EBN)	Jansky et al., 2009
S. neocardenasii	Tomatines, glandular trichomes	Antibiosis	2X	Dimock et al., 1986
S. opolcense			2X (2EBN) 4X (4EBN) 6X (4EBN)	Pelletier et al., 2001
S. trifidum	Toxic compounds	Antibiosis/antixenosis	2X (1EBN)	Sikinyi et al., 1997; Pelletier et al., 1999, 2001
S. okadae	Tomatines	Antibiosis	2X	Pelletier et al., 2001
S. acroglossum			2X (2EBN)	Pelletier et al., 2001; Pelletier, 2007
S. chomatophilum			2X (2EBN)	Pelletier et al., 2001; Pelletier, 2007
S. paucissectum			2X (2EBN)	Pelletier et al., 2001; Pelletier, 2007
S. piurae			2X (2EBN)	Pelletier et al., 2001; Pelletier, 2007
S. tarnii			2X	Pelletier et al., 2001; Pelletier, 2007

Adapted from Maharijaya and Vosman (2015) and Jansky et al. (2009). Ploidy and endosperm Balance Number (EBN) information was derived from Spooner and Hijmans (2001).

Kennedy and Sorenson, 1985; Dimock et al., 1986; Gregory et al., 1986; Lapointe and Tingey, 1986; Carter et al., 1989; Tingey, 1991; Pelletier et al., 1999; Pelletier and Dutheil, 2006; Tian et al., 2012). This mechanism of resistance reduces the mobility of insects (both adults and larvae) on the leaf surface through trichome secretion (Gibson, 1971; Gibson and Turner, 1977; Tingey and Gibson, 1978; Dimock and Tingey, 1987) or discharge of metabolites after mechanical disruption of trichomes (Tingey and Laubengayer, 1981; Ryan et al., 1982). Trichome-mediated resistance has been found in several wild potato species (Flanders et al., 1992; Pelletier et al., 1999) including S. *neocardenasii* (Dimock et al., 1986), *S. polyadenium* (Tingey and Gibson, 1978), *S. tarijense* (Gibson, 1971) but a majority of our knowledge is derived from experimentation focused on *S. berthaultii* accessions and introgression lines (Wright et al., 1985; Groden and Casagrande, 1986; Dimock and Tingey, 1987; Neal et al., 1989; Bonierbale et al., 1994; Yencho et al., 1998).

Trichome-associated resistance to *L. decemlineata* in *S. berthaultii* is conditioned by the presence of two types of trichomes on leaves and stems of the plant. Type A trichomes are the smaller of the two, exhibiting length between 120 and 210 µm and possess a tetralobulate head with a diameter of 50 to 70 µm (Gregory et al., 1986). When ruptured by mechanical disruption, Type A trichomes release polyphenol oxidase enzyme (PPO) which rapidly polymerizes the substrates contained within the trichome head (Ryan et al., 1982; Kowalski et al., 1992). The accretion of hardened, polymerized exudate adheres to the tarsi and mouthparts of insects which reduces their mobility and can trap smaller insects, like aphids, to the leaf surface (Gibson and Turner, 1977; Tingey and Gibson, 1978). Type B trichomes are much larger (600–950 µm) and secrete a viscous fluid droplet on the tip of each stalk (diameter 45 µm). Exudates from type B trichomes contain fatty acid esters of sucrose, that vary by the number (and position) of linkages and fatty acid chain length across accessions (King et al., 1986, 1987a,b). Solvent removal of exudates or mechanical removal of trichomes does not attenuate the repellent effect of *S. berthaultii* leaves in choice assays but leads to increased feeding and decreased mortality of larvae relative to *S. tuberosum* (Dimock and Tingey, 1988; Neal et al., 1989; Yencho and Tingey, 1994). Evidence from Neal et al. (1989) suggests that type A trichomes are a fundamental requirement for *L. decemlineata* resistance but the presence of type B trichomes may have a synergistic effect; whereas Yencho and Tingey (1994) concluded that both mechanical and chemical mechanisms likely contribute to *L. decemlineata* resistance in *S. berthaultii*.

From a breeding perspective, trichome mediated insect resistance is attractive as it may provide durable resistance (França and Tingey, 1994) to multiple insect species simultaneously (Gregory et al., 1986). At the genetic level, trichome mediated resistance can be introgressed into domesticated potato (Mehlenbacher et al., 1983; Wright et al., 1985; Plaisted et al., 1992), and behaves as a quantitatively inherited trait (Mehlenbacher et al., 1983). Introgression of resistance from *S. berthaultii* has resulted in the release of several potato clones from the breeding program at Cornell University NYL 235-4, Q174-2, and NYL 123 (Plaisted et al., 1992; de Souza et al., 2006; Malakar-Kuenen and Tingey, 2006). Quantitative genetic studies support an additive, multigene inheritance model, where *L. decemlineata* resistance is associated with trichome characteristics including density and chemical composition (Bonierbale et al., 1994; Yencho et al., 1996).

Complimentary studies aimed at characterizing the inheritance of trichome related traits and *L. decemlineata* resistance in reciprocal *S. berthaultii* × *S. tuberosum* hybrid backcross populations indicate that traits exhibits some shared and some unique features to their genetic architecture (Bonierbale et al., 1994; Yencho et al., 1996). Inheritance of insect resistance is clearly a multi-locus trait that exhibit differences in penetrance based upon how trait values are skewed differentially between backcross parent (Bonierbale et al., 1994; Yencho et al., 1996). The number of type A trichomes is largely controlled by the inheritance of *S. berthaultii* alleles on chromosome 6 (dominant) and 10 (recessive), which combine to describe up to 63% of variation in a *S. berthaultii* backcross population (Bonierbale et al., 1994). PPO concentration is also a multi-locus trait with QTL on chromosomes 2, 5, 8, and 11 potentially contributed to enzyme abundance (Bonierbale et al., 1994). Inheritance of type B trichomes is clearly recessive as type B trichomes are not observed in *S. tuberosum* backcross populations derived from *S. berthaultii* × *S. tuberosum* hybrids (Bonierbale et al., 1994). The presence of sucrose ester droplets and abundance of type B trichomes are controlled by a major QTL located on chromosome 5 and additional QTL located on chromosome 1, 2, and 4 (Bonierbale et al., 1994). These plant characteristics seem to directly relate with *L. decemlineata* feeding and reproductive presence in backcross populations, which are influenced by no fewer than four QTL located on chromosomes 1, 5, 8, and 10 (Yencho et al., 1996). When the results of both Bonierbale et al. (1994) and Yencho et al. (1996) were overlaid, *L. decemlineata* resistance as measured by Yencho et al. (1996) exhibited QTL located on 1, 5, 10 in a *S. berthaultii* backcross population whereas QTL associated with type A trichome characteristics (Bonierbale et al., 1994) were associated with QTL 1, 2, 4, 5, 6, 10, and 11 in the same population. Whereas, in a *S. tuberosum* backcross population fewer QTL were identified and the only major overlapping QTL was associated with PPO activity on chromosome 8 (Yencho et al., 1996). Largely due to the thoroughness of these investigations (Bonierbale et al., 1994; Yencho et al., 1996), it is suspected that chemical resistance also may play a role due to segregation of glycolalkaloid content associated with the *S. berthaultii* background (Yencho et al., 1998).

Although great strides have been made toward the identification, introgression, and genetic mapping of *L. decemlineata* resistance mechanisms into breeding lines, there is still much work to be done. Currently no *L. decemlineata* resistant cultivars have been widely accepted and planted on large acreage (Grafius and Douches, 2008). Linkage mapping is an indispensable tool for mapping quantitative traits, but other complimentary methods including genome-wide association studies (Sharma et al., 2018; Yuan et al., 2019) or quantitative evolutionary genetic methods (Hardigan et al., 2017; Li et al., 2018) can have a great impact identifying major allelic variants within populations/species groups. Comparative genomics with other *Solanum* spp. has long been perceived as a method to leverage our knowledge of biochemical genes across species (Cárdenas et al., 2015) and has been used to identify shared components responsible for glycoalkaloid biosynthesis (Itkin et al., 2011; Cárdenas et al., 2016).

Little is understood about the mechanisms of resistance present in other species outside of *S. chacoense* and *S. berthaultii* or the genetics underlying these traits. This is particularly apparent for germplasm from the endosperm balance number 1 clade in potato (Carter, 1987; Flanders et al., 1992; Jansky et al., 2009; Pelletier et al., 2011). Consistently high levels of resistance in field screens but the mechanisms responsible of this quality are less tractable to breeders focused on cultivated *S. tuberosum* due to crossing barriers. Bridge crosses (Yermishin et al., 2014) and somatic hybridization (Jansky et al., 1999) are tools that researchers have used to introduce these traits into backgrounds compatible with cultivated potato (Jansky, 2006).

Transgenic potatoes thru genetic engineering has focus on pest resistance (Michaud et al., 1993; Alyokhin and Ferro, 1999; Grafius and Douches, 2008; Šmid et al., 2013). In 2013, Cooper et al. (2004) combined genetic engineering and traditional breeding testing feeding, biomass accumulation, and mortality on three populations of *L. decemlineata* including a Bt cry 3A-selected population which apparently conferred elevated resistance in potatoes. Mi et al. (2015) also reported excellent results expressing cry3A genes. However, *L. decemlineata* adapts quickly (Zhu-Salzman and Zeng, 2015). Jin et al. (2015) developed large-scale tests of natural refuge for delaying cotton bollworm (*Helicoverpa armigera* Hüber) resistance to transgenic Bt crops that could be used for *L. decemlineata*. Li et al. (2017) also studied the function and effectiveness of natural refuge in Insecticide Resistance Management strategies for Bt crops but more studies are still needed. Ma et al. (2020) reviewed the benefits of RNA interference (RNAi) tested for *L. decemlineata* where target genes, efficiency, and factors affecting RNAi efficiency against this pest were discussed.

CURRENT BREEDING EFFORTS: NORTHWEST CASE STUDY

Maharijaya and Vosman (2015) suggest that breeding potato for resistance against *L. decemlineata* will benefit from information obtained using new, higher throughput screening methods. This has proven true in row crops, particularly as it relates to quantitative genetics and marker assisted selection. Improvement of crops using quantitative genetics requires identifying biological association between the plant phenotype of interest (insect resistance) and genetic or biochemical markers that can be used to select for that trait (Bernardo, 2019; Paudel et al., 2019).

Oftentimes the number of measurements required for genetic mapping, particularly in field studies, substantially outnumber the resources that can be allocated to perform this task by any single research group. In such cases, collaborative efforts between domain experts (entomology, breeding, remote sensing, analytical chemistry etc.) can be hugely beneficial. Small scale field studies can help us assess our ability to evaluate insect preference. Such information is critical for understanding both the insect pressure at a given trial location and how the aggressiveness of foliar consumption varies between field seasons.

Human index scoring of insect mediated defoliation is a relatively quick and accurate measurement, however as the clone number within a trial and number of field sites increases, our ability to accurately record this data becomes limiting. Data collection using multispectral sensors fixed to sUAS have been proposed as a scalable method to estimate insect damage in numerous crops (Puig et al., 2015; Mahlein, 2016; Vanegas et al., 2018) including potato (Hunt et al., 2016; Hunt and Rondon, 2017; Théau et al., 2020). When combined with ground truth measurements, multispectral data collected using sUAS can provide high-resolution, quantitative data on plant performance on larger scales and at greater frequency than could possibly achieved by human observation alone (White et al., 2012). This sort of standardized measurement is particularly attractive for multi-location field trials where scoring of insect mediated defoliation must be measured by members of different research groups and with high spatiotemporal resolution. Unfortunately, spectral measurements can be influenced by many confounding factors including, plant genotype, plant developmental stage, management practices within the trial, and environmental variables across time (White et al., 2012; Hunt et al., 2016; Khot et al., 2016; Chivasa et al., 2020; Théau et al., 2020). So, more research is needed to ascertain how reliable these measurements are at measuring insect damage specifically, across locations and field seasons.

We believe that multiscale measurement strategies, that begins with field screening of segregating populations or wild germplasm to narrow research focus can be useful and are an efficient use of resources. Identifying particularly resistant or susceptible germplasm, will help researchers focus on studying the mechanisms of resistance in much greater detail though application of some of the more difficult, expensive, and time demanding assays described in this article.

AUTHOR CONTRIBUTIONS

SR and MF planned the idea of the review and wrote entire manuscript. SR designed the framework of the review. AT contributed with the writing and editing and providing information for **Table 3**. TO provided editing and organized literature citation. GS contributed on editing and organizing of literature citation. All authors contributed with the final version of this manuscript.

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